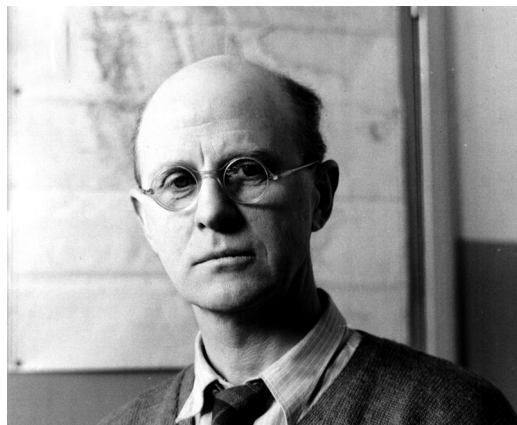


*Classics in physical geography revisited*



## **Elton, C.S. 1958: *The ecology of invasions by animals and plants*. London: Methuen.**

The study of invasions of organisms following their transfer by humans to areas far outside the reach of natural dispersal mechanisms has grown enormously in recent decades and is now a prominent subdiscipline of ecology (Simberloff, 2004; Davis, 2006; Pyšek *et al.*, 2006; Richardson and Pyšek, 2006; Lockwood *et al.*, 2007). The rapid growth in interest in invasion biology has mirrored the escalation in the extent of invasions and the magnitude of impacts attributable to invasive species. Increasingly, however, invasions are studied as experiments in biogeography – to gain insights on factors and processes that control diversity and distributions at different spatial scales and where manipulative experiments are impractical (Richardson, 2006; Palmer, 2006).



**Figure 1** Charles Sutherland Elton (1900–1991) (reproduced courtesy of the Zoology Department, University of Oxford)

In the nineteenth century, several pioneering naturalists – notably Darwin, De Candolle, Hooker and Lyell – mentioned invasive species in their writings. Naturalized and invasive species were, however, essentially curiosities at the time and not a major threat to global biodiversity. Charles S. Elton's (1958) book *The ecology of invasions by animals and plants* is recognized as the starting point for focused scientific attention on biological invasions. The book, noted for its 'clarity of ... writing, the wonderful and quaint illustrations, and the importance of the message' (Mooney, 1998; see also Simberloff, 2000) has been acclaimed variously as 'an accessible and enduring classic', the 'bible of invasion biology', a 'classic book', 'the cornerstone work in [invasion ecology]', an 'invasion classic', a 'magisterial book', 'one of the most forward-looking publications in ecology', a 'pioneering work' and a 'seminal work'. It has been cited more than 1500 times in the international literature listed on the Web of Science to date, more than any other publication on invasions (Pyšek *et al.*, 2006). It is still regularly cited – at least 117 times a year since 2000. Like invasions themselves, the growth of publications on invasions has been explosive. The lofty status and longevity of Elton's book is perhaps surprising, given the style of the writing. It is essentially a short popular science book that grew from a series of radio talks on the BBC in 1957. What ingredients have made it so influential and does it deserve this status?

Here, we explore briefly the extent to which Elton's (1958) book set the agenda

for what is now known as invasion ecology. Why did it take several decades for research on the topic to really take off after the publication of Elton's book? Which of Elton's bold generalizations have held up to scrutiny? Which are still receiving research attention? Where was Elton wrong? Is the book still a rich source of ideas for researchers in the field? Should the book still be prescribed as primary reading for students? As part of our attempt to deal with these issues, we did an email survey of the most influential authors in the field of invasion ecology to gauge opinions on several key topics/issues relating to Elton's book (see Appendix). Their observations guided our thinking and further reading.

What did Elton cover in the nine chapters and 181 pages that make up *The ecology of invasions by animals and plants*? The book starts with a brief overview entitled 'The invaders', describing 'one of the great historical convulsions in the world's fauna and flora', in which Elton gives a preliminary sketch of some of the issues he regarded as crucial for understanding these 'ecological explosions'. Chapter Two provides the important global biogeographic perspective. Here, Elton discusses the evolution of the world's biota and the importance of isolation in generating and maintaining biodiversity: 'Wallace's realms: the archipelago of continents'. The next chapter describes the breakdown of isolation through the movement of organisms around the world by humans. He discusses numerous case studies covering a wide taxonomic array from all parts of the world and considered trends and motives that result in the widespread transport of organisms to areas well outside their natural ranges – 'The invasion of the continents'. Chapters Four and Five describe features of invasions of islands and the oceans, respectively. In Chapter Six, Elton begins to explore the mechanisms of invasions in a short essay entitled 'The balance between populations'. This theme is continued in Chapter Seven which describes various ways in which invasive species can

profoundly alter food chains in ecosystems. The last two chapters deal with the 'so what?' In Chapter Eight, Elton discusses the various reasons for conserving nature, and how the invasions that he has described in the book threaten humankind's ability to conserve biodiversity. In the final chapter, Elton poses philosophical questions (profound for the time) relating to economical, ethical and other reasons for 'the conservation of variety' in the face of looming invasions and biotic homogenization.

Elton's views were, of course, shaped by his particular experiences and interests. He was English, and although he did some work in Lapland and Spitsbergen, most of his fieldwork was in the English countryside. He did travel to North America, but never visited the tropics or the Southern Hemisphere. Nonetheless, the book collects examples from around the world. Elton clearly tried to achieve even global coverage, and succeeded to a large degree, but for most of the world his coverage was based on the literature and correspondence. Elton was a zoologist, and animals are given prominence in his book. Of the 195 organisms identified to at least genus level in the index, 169 (87%) are animals; of these 51% are arthropods, 27% vertebrates, and the rest molluscs. Plants, although featured in the book's title, are given scant coverage (only 18 species of vascular plants in the index), while other groups, in keeping even with current research in invasion ecology (Wilson *et al.*, 2007a), get much less coverage: fungi (5 spp.), protists (2 spp.) and red alga (1 species). However, the bias in favour of animals does not substantially reduce the generality of his conclusions. The book presents a 'big picture' synopsis that cuts across traditional biological domains of the day.

To us, the overriding feature of Elton's book, and the primary reason for its landmark status in invasion ecology, is simply that it brought together previously disparate themes (biogeography, conservation biology, epidemiology, human history, population

ecology, and others) to show the true global scale and the severe and escalating implications of biological invasions for life on earth. He placed the phenomenon in the context of ecological understanding of the time, and provided a map for new research directions. Ecologists today tend to forget that 50 years ago ecology was the domain of a few biologists who were concerned largely with natural ecosystems, and who sought, as a rule, to exclude things 'unnatural' from their studies. The escalation of biological invasions in the 1950s, much of it the result of European colonization of the globe a century or more before, was but one symptom of emerging changes to our planet that were about to force ecologists to vacate their comfort zones and to address issues relating to sustainability in the face of rapid human-mediated global change (Mooney, 1998). One must consider the ecological research milieu at the time that Elton penned the book. The nascent science of ecology was largely descriptive or qualitative. Elton was a pioneer in the field of theoretical and quantitative ecology, but was one of the first internationally acclaimed ecologists to apply the science to influence policy and to 'be useful' (Lawton, 2007).

Although Elton's 1958 book was by no means a scientific treatise or textbook, several arguments invoke far-reaching concepts and hypotheses. Probably most notable are the arguments he advanced to show that complexity in the arrangement of trophic webs in a community causes greater species population stability through time than when trophic webs are simpler. This issue featured in Elton's (1927) *Animal ecology* volume, and was addressed by other authors in the 1950s (eg, MacArthur, 1955), but was given new life with reference to introduced organisms in his 1958 publication. The profundity of these concepts was rapidly grasped by leading ecologists. Debate around this issue defines one of the hottest topics in invasion ecology to this day – the link between various measures of diversity at different spatial scales and

the capacity of an ecosystem to accept new members. There are several components of this general issue; Elton set out six lines of argument (see Watt, 1968: 41; Ives, 2007: 99). Most subsequent formulations combine several elements of Elton's reasoning in, for example, the 'simple-community hypothesis' (Johnstone, 1986), the 'balance of nature' hypothesis (eg, Cronk and Fuller, 1995), the 'diversity-stability hypothesis' (also termed the 'diversity-invasibility hypothesis') *sensu* Tilman (1999), or the 'biotic resistance' hypothesis (see Simberloff and von Holle, 1999) for a history). For a comprehensive review of some of the main subissues related to this topic and progress in research in these areas, see Fridley *et al.* (2007).

Although Elton's book was lauded as an important contribution soon after its publication (eg, Saville, 1960; Waloff, 1966; Pianka, 1967), it did not immediately lead to a significant rallying of brainpower to address issues *directly associated with invasions*. As mentioned above, much of ecology at the time was obsessed with 'natural' ecosystems and invasions were seen as noise – to be avoided as far as possible in field studies. Background noise. Elton's 1958 book, and particularly his diversity-stability ideas, did, however, influence important theoretical ecologists of the day, notably Robert May (May, 1973). May's work, using mathematical models to compare ecological communities with few species with those with more species, found that 'there could be no such simple and general rule [as suggested by Elton]; all things being equal, complex systems are likely to be more dynamically fragile' (May, 2001). He showed that there is no automatic connection between complexity and stability as suggested by Elton's arguments. Nonetheless, we must realize that food webs in the natural world are the winnowed products of evolution, and as such represent a very special subset of 'complex systems' (R.M. May, personal communication, 2007). May's work and other recent studies (eg, Naeem *et al.*, 2000) have ensured sustained research

interest in this topic. One of Elton's most fundamental contributions to general ecology was his formulation of concepts relating to the ecological niche. Invasions clearly gave him fertile ground for deliberation on the role of niches in structuring communities. The 'Eltonian niche' (Beals, 1972) finds expression in the 1958 volume, and still enjoys attention in the search for robust theoretical frameworks for biological invasions (eg, Shea and Chesson, 2002). Elton's generalization that islands are more invaded than mainland areas has held up to scrutiny (see Pyšek and Richardson, 2006, for a status report for research on plant invasions).

Another milestone book on invasions, the edited volume *The genetics of colonizing species* (Baker and Stebbins, 1965) appeared soon after Elton's book. Whereas Elton's book took a 'conservation and environmental approach', the Baker and Stebbins volume adopted a 'more value-neutral and more strictly scientific approach' (see Davis, 2006: 50–51 for further discussion on important differences between the two works). A detailed assessment of the separate and linked legacies of these two publications is overdue.

It was only in the 1980s, largely as a result of the international SCOPE programme on biological invasions (Drake *et al.*, 1989), that invasions clearly began their march to centre stage in the theatre of mainstream ecology (Pyšek *et al.*, 2006). A central reason for the initiation of the Scientific Committee on Problems of the Environment (SCOPE) programme, besides the conservation imperative, was the emerging realization that the increasingly widespread invasions across the globe seemed to be at odds, in some respects, with Elton's generalizations. For instance, Mooney (1998) describes how the realization that alien trees and shrubs readily invade undisturbed South African fynbos, in contrast to Elton's predictions, was a key observation that led to the initiation of the SCOPE programme. This international initiative provided the framework for substantial investments worldwide in research on biological invasions, and to the proliferation of

publications on the topic. The lag phase in the development of invasion ecology was over. Many publications that emanated from the SCOPE programme drew on Elton's concepts and generalizations and, to a degree, implicitly used Elton's findings as a null model. As mentioned above, the diversity-stability hypothesis in its various guises and formulations continues to take up many pages of journal space, probably because it is now easier to test empirically using accumulating data from different regions and over various spatial scales (eg, Chytrý *et al.*, 2005; Stohlgren *et al.*, 2006). The role of disturbance in initiating and sustaining invasions remains an important focus of research. Recent work points to a complex relationship between disturbance and invasibility (Davis *et al.*, 2000); certainly, Elton's one-dimensional notion that only highly disturbed ecosystems are invaded is too simplistic (Huston, 2004). Many, indeed most, of the hottest issues in invasion ecology have emerged as important post-Elton, or were mentioned only superficially by Elton. For instance, the crucial roles of facilitation, dispersal dynamics (including long-distance dispersal) propagule pressure, phenotypic plasticity and rapid evolution are now recognized as critical determinants of invasiveness and invasibility (Richardson and Pyšek, 2006). Why did Elton not deal with these issues? Part of the reason lies in the particular collection of case studies he assembled for his narrative and also the stage of invasions worldwide. Another reason is that the tools available for mapping and analysing data were not advanced enough to uncover complex relationships. Only with recently acquired large databases and advanced computing power have we been able to do the complex spatial analyses that are required to unravel interactions that can explain levels of invasiveness (eg, Wilson *et al.*, 2007b). Ditto for unravelling the dimensions of biotic homogenization at different spatial scales (Cassey *et al.*, 2007). Recent advances in molecular ecology have opened doors for insights on aspects of invasion ecology that

Elton would never have dreamt of. New vectors and pathways of introduction and dissemination have emerged or increased in importance post-Elton (eg, Thuiller *et al.*, 2005; Ricciardi, 2006). The new disciplines of resource economics and risk analysis are now crucial areas of research in invasion ecology (eg, Perrings *et al.*, 2005).

Davis *et al.* (2001: 98) argued that Elton 'may have unintentionally handicapped [invasion ecology's] subsequent development' by trying to separate the study of invasions from ecology in general. In particular, they feel that Elton regarded 'invaders as a distinct group of organisms and invasion as a process distinct from the colonizations that are an integral part of many successions'. Although there is no doubt that invasion ecology has not drawn adequately on advances in related fields such as conservation biology (eg, van Kleunen and Richardson, 2007), palaeoecology (Petit *et al.*, 2004), restoration ecology (Hobbs and Humphries, 1995), weed science (Booth *et al.*, 2003; Richardson, 2003), and succession ecology (Davis *et al.*, 2005), we see no reason to place the blame for this at Elton's door. To the contrary, we subscribe to Berry and Scriven's (2005) view of Elton, also in his 1958 book, as a visionary scientist who fostered considerable cross-disciplinary synergy (see also Appendix, question 13).

How is Elton's book viewed by the most active and influential invasion ecologists today (see Appendix)? Most of them have read Elton's book (most own a copy, have reread it recently, and cite it in their publications and lectures), although less than half state that Elton's book was a major inspiration for their interest in invasions. More than half of them consider the book to be THE foundation of invasion ecology. Opinion is divided on whether Elton's book is still a major source of ideas and concepts in the field (several of those who said 'yes' work on biotic resistance/stability issues; many of those who said 'no' work on processes and determinants of invasiveness and invasibility) and whether the book is still a good general reference on invasions (more than half would

rather cite more recent works which provide more up-to-date assessments). Almost all respondents felt that there are indeed specific issues in the book that are still relevant for researchers today. The most obvious specific topic raised by Elton that is still considered 'hot' is the 'diversity/stability issue' discussed above. Elton's book is still considered useful (if not essential, primary) reading for students of invasion ecology. The most popular phrase to describe Elton's contribution is 'a classic book'.

Charles Elton's *The ecology of invasions by animals and plants* has served invasion ecology well and continues to provide absorbing reading for anyone seriously interested in the field. Keeping track of the developments and cutting-edge topics in invasion ecology is now a formidable challenge. To this end, the excellent book by Lockwood *et al.* (2007) and the journals *Biological Invasions* and *Diversity and Distributions* are good starting points for newcomers to the field.

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## Appendix

Questions asked of 22 top invasion ecologists (highest-ranking senior authors in the survey of the most influential papers in invasion ecology (1981–2003); Pyšek *et al.*, 2006: Appendix I) in an email survey conducted in April/May 2007. Answers are z, with brief notes on the main discussion points raised in the email survey. Respondents were: Ragan M. Callaway; Jim L. Carlton; Andrew Cohen; Mick J. Crawley; Carla M. D'Antonio; Mark A. Davis; Richard J. Hobbs; Jonathan M. Levine; David M. Lodge; W. Mark Lonsdale; Richard N. Mack; Ingrid M. Parker; David Pimentel; Petr Pyšek; Sarah H. Reichard; Marcel Rejmánek; David M. Richardson; Katriona Shea; Tom J. Stohlgren; David Tilman; Peter M. Vitousek; and Mark Williamson.

1. Have you ever read Elton's book (cover to cover)? **YES (20/22)**; NO (2/22)
2. Have you read it recently (in the last 10 years)? **YES (15/19)**; NO (7/22)
3. Do you own a copy of the book? **YES (20/22)**; NO (2/22)
4. Do you regularly cite this book in your publications? **YES (16/22)**; NO (6/22) [several respondents who replied 'yes' provided qualifications, eg, 'mainly for historical reasons', 'mainly in my older publications']
5. Was this book a major inspiration for your interest in biological invasions? **YES (8/22)**; **NO (14/22)** [One responded: 'Yes, but often in a negative way. I didn't believe the stuff about geographic spread rates, and I was frustrated by the lack of good stuff on plant invasions']
6. Do you regard the book to be THE FOUNDATION of invasion ecology? **YES (15/22)**; NO (6/22); YES/NO (1/22) [Several respondents qualified their answers at length, eg, 'Yes, ONE of the foundations', 'YES, in the sense that it marks the great awakening to this topic among many ecologists, NO in the sense that the topic's few mavens had already long before established a foundation' 'No, Darwin's observations on islands predates Elton's by a century']
7. Is Elton's book still a major source of ideas/concepts in the field? **YES (11/22)**; NO (11/22) [Several respondents provided lengthy qualification, eg, 'No, there is little population dynamics in it. The dispersal theory is very out of date'; 'No, not for new ideas'; 'Yes, more so for me now, actually']
8. Is Elton's book still a good reference to cite as a general reference (eg, 'invasions are a global problem that threatens biodiversity')? **YES (10/22)**; **NO (12/22)** [Qualifications included: 'No, I would cite more current literature'; 'No, much more specific, as well as well documented, comprehensive information has been assembled']

9. Are there SPECIFIC ISSUES/CONCEPTS in Elton's book that you think are particularly relevant/important for researchers today? **YES (18/22)**; NO (4/22) [Respondents that answered NO felt that Elton's main contribution was to alert ecologists to general issues ('the big picture') and that the book has limited relevance for details on specific issues]
10. If you answered YES to question 9, please list up to three issues/concepts for which Elton's book is still a seminal reference. Main answers were: **The diversity/stability issue ['biotic resistance'] (7)**; the global scale of the problem/globalization (3); the susceptibility of islands to biological invasions (4); the relevance of conservation to human societies (2); the idea of homogenization of biotas (2); the assembly of case studies of invasion as a means of analysis and generalization (1); biogeographical context for thinking about invasions (1); the role of species interactions in mediating invasions (1); detailed mapping of spread of invasive species (1).
11. Would you still recommend Elton's book as ESSENTIAL READING for students reading courses in invasion biology? **YES (14/22)** NO (8/22) [Most respondents who replied NO added something like 'but in the extended reading list' or 'useful supplement only'. Most of those who responded YES, gave as the main reason 'It is essential to know the history of the study of invasions'; fewer gave as a reason 'There are still valuable lessons to be learnt from the book']
12. Which word/phrase would you think best describes Elton's book? 'pioneering work' (3) 'one of the most forward-looking publications in ecology' (3); **'a classic book' (8)**; 'a magisterial book' (0); 'an accessible and enduring classic' (2); a 'seminal work' (2); '[the] bible of invasion biology' (0); 'the cornerstone work in [invasion ecology]' (0)
13. Do you think that the claim that Elton's book served to dissociate invasion ecology from the rest of ecology is justified? YES (1/22) **NO (18/22)** No answer (3/22)